NORTH AMERICAN PARASITIC COPEPODS BELONGING TO THE FAMILY CALIGIDÆ.

PARTS 3 AND 4. A REVISION OF THE PANDARINÆ AND THE CECROPINÆ.

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INTRODUCTORY.

The present is the sixth paper in the series based upon the collection of the U. S. National Museum and finishes the family Caligidæ. For many reasons a large amount of careful and painstaking collating has been rendered necessary before this paper could be published. And in consequence, as its title indicates, it has taken the nature of a thorough revision of the two subfamilies which it includes. Such a revision was found to be absolutely demanded for any intelligent discussion of the group, and especially for its accurate systematization.

In the first place, up to the present time we have been acquainted with both sexes of but one or two species in the entire subfamily Pandarinæ. Of all the other forms either the male or the female have been described alone.

This has been due not to any scarcity of the missing sex, as might be supposed, but to the fact that when found it was located elsewhere on account of the great morphological dissimilarity between the sexes. So that we find repeatedly the anomaly of a female classified under one genus and subfamily, while the male is located under an entirely different genus, and often in another subfamily.

Furthermore, all previous attempts to bring together the sexually separated species have been confined to individual cases or to closely related forms. And there has been in these attempts such an utter disregard of morphological and developmental data that they have only served to render the confusion worse confounded. To the best of the author's knowledge the present paper is the first to systematize

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the group upon a morphological basis. As will be seen the structure in a few instances supports the suggestions that have been made regarding the identity of sexes, while in the great majority of cases it is directly opposed to them. It is obvious, however, that any suggestion of species identity which is not supported, or which may even be contradicted by the anatomy of the two sexes, is worthy of very little consideration.

And it is really surprising how much similarity a careful examination reveals when we remember that the two sexes have been considered generically distinct. The differences are found to be much more apparent than real, and this is particularly true of the appendages which afford a ready clew for the determination of the genera, as can be seen from the key which follows (p. 345).

There is of course no expectation of being able, in this initiatory effort, to reach a final conclusion respecting all the *Nogaus* species. Considerable additional information will be needed before that becomes even possible. But at least a good beginning can be made, and the treatment of the species can be placed upon a rational and scientific basis, which will yield good results in the future.

Each male has been included in the genus to which it belongs, so far as this is positively known, and its characteristics have been given under the genus diagnosis.

There are here described twenty species, of which one is new to science, namely, *Echthrogaleus torpedinis*, while two others, *Echthrogaleus denticulatus* Smith and *Nesippus alatus* Wilson, are figured for the first time, the latter including both sexes.

In addition the males of eight of the other species have been definitely located, described, and figured, four of them being new to science, while the other four have been boarding around among the various genera as was formerly the custom with the teachers in our old-fashioned country schools.

The males of the three species belonging to the Cecropinæ, of *Gangliopus pyriformis*, and of *Pandarus bicolor* were already known so that we now have the males of 14 of the 20 species, including at least one for every genus.

And lastly, much the hardest task of all, in the discussion of the genus *Nogaus*, which is made up entirely of males, 34 species, described by half as many authors and in seven different languages, have been carefully contrasted with one another and with the types here established, so far as the data given made this possible.

It has been found necessary to change the names of two genera on account of preoccupation. The name *Lepidopus*, proposed by Dana in 1852, had been used by Gouan for a fish genus in 1770. In its place is suggested the name *Pholidopus* which has the same meaning, namely, scale-footed.

The name *Stasiotes*, proposed by Wright in 1877, had been used by Jan for a snake genus in 1862. In its place is suggested the name *Prosaetes*, from προσαίτης, a beggar, who torments one by his persistence.

A complete life history is also presented by using different stages of development from different genera, but as none of the developmental stages have ever been described even this is a considerable advance.

Part 3.—THE PANDARINÆ.

ECOLOGY.

The Pandarinæ are peculiarly shark parasites, the genera and even the species, almost without exception, infesting some one of the numerous selachians along our coasts. In general the females remain throughout life fixed in the same position on their host, and even the males are rarely found swimming about freely. And yet upon occasion, as will be seen later, these males can swim as well as any of the Caliginæ. Hence it is not a case of necessity but one of choice that keeps them in close proximity to the fixed females.

In this connection Hesse writes:[a]

> Les poissons sur lesquels on les trouve n'étant pas, comme ceux des autres espèces, enduits d'une sécrétion mucilagineuse qui, en lubrifiant la peau, la rend plus souple et plus pénétrable et facilite ainsi les fonctions des organes destinés à la perforer. Privés de ces avantages et insuffisamment fixés sur une enveloppe épaisse et coriace, ils ne tardent pas, lorsqu'ils sont sortis de l'eau, à s'en détacher et à tomber à terre, ou dans le fond des bateaux, et alors, à raison de leur extrême petitesse, il est bien difficile de les retrouver.

This statement might give the impression that the Pandarinæ are outcasts among the parasites, unable to find anything better in the way of hosts, and so compelled to put up with these thick-skinned sharks. But such does not seem to be the case; the shark's skin is tough, but is not particularly thick for so large a fish, and it is certainly covered with mucus the same as that of other fishes. It is therefore as easy to penetrate as the skin of a fish covered with heavy scales.

Furthermore, as Hesse himself says, immediately after the passage quoted, these Pandarinæ seek out those places on the shark's body where the skin is the thinnest, such as the fins, the inside of the operculum, the border of the anal and genital orifices, and even the eyes. In fact this same preference is shown by all the Caligidæ, and is just as pronounced on a scaly fish as on these selachians, for the skin in the localities mentioned is always soft and tender enough, even on a shark, to be easily penetrated, especially by such large parasites as the Pandarinæ. Hence the reason implied by

[a] Annales des Sciences Naturelles (6), XV, Article 3, p. 39.

Hesse, and stated clearly in a footnote at the bottom of the page just referred to, can not be the only one. He says in the footnote:

C'est sans doute à raison de la plus grande épaisseur de leur peau que je n'ai jamais rencontré ces parasites sur les *Scyllium canicula, catulus* et *annulatus,* qui cependant sont des Squales que l'on trouve plus fréquemment que les autres dans notre localité.

It is very doubtful if the skin of these sharks he mentions is any thicker than that of the dusky shark, *Carcharhinus obscurus,* and other large sharks of our own coasts which are commonly infested with these parasites. And even if it were thick and tough enough elsewhere, it would still be thin and soft at the localities mentioned, and easily penetrated by the sharp probosces of these large Pandarids. Some other reason must be found to account for the lack of parasites on the sharks mentioned.

FIG. 1.—PHOTOGRAPH OF DORSAL FIN OF SAND SHARK, SHOWING BOTH SEXES OF PANDARUS SINUATUS. IN THE LOWER BUNCH THE PARASITES ARE ENTIRELY COVERED WITH ALGÆ.

Again Hesse writes:[a]

J'ai, en effet, visité, avec le plus grand soin et depuis un assez grand nombre d'années, les poissons de toutes les espèces qui fréquentent nos côtes et je suis parvenu à trouver vingt *Caliges* différentes, ainsi que dix *Trébies;* et toutes, sans aucune exception, ont été recueillies sur le corps ou sur les branchies de poissons à peau molle, conséquemment autres que les *Squales.*

The sharks along our Atlantic coast must be very different from those on the coast of France, since the author has found two of the Argulidæ, *Argulus laticauda* and *A. megalops,* two of the Caliginæ, *Caligus rapax* and *Lepeophtheirus edwardsi,* and two of the Euryphorinæ, *Alebion gracilis* and *A. glaber,* very commonly upon them. The two last mentioned species are practically confined to the Dogfish and Sand Shark, and are found all over the outside surface of these fishes, apparently never hunting for any thin places in the skin.

Furthermore the Caliginæ are common also upon Skates and Rays, whose skin is as tough and leathery as that of the sharks, at least six species being found on these fish.

We may reasonably conclude, therefore, that the sharks are selected by these parasites as their chosen hosts. And there is no reason for believing that they do not prove as satisfactory as any bony fish (fig. 1).

[a] Same article, p. 30.

We have already stated that the females remain throughout life fixed in one position upon their host. This is true of all the genera belonging to the subfamily and constitutes a fourth step in degeneration as well marked as the three which have preceded it.[a]

The last three of these steps, however, and a part of the first one, have been confined to the female, while the male has escaped their influence.

As a result we find in the present subfamily the greatest sexual dissimilarity in the entire family of the Caligidæ.

Indeed, the two sexes of every genus in the Pandarinæ are so unlike that the males have been considered a separate genus from the females. And not only so, but the males of all the genera have been made congeneric, and grouped together under the single genus "*Nogagus*." Furthermore, this male "genus" has been placed by the great majority of writers in the subfamily Caliginæ rather than in the Pandarinæ, where the females all belong. This will be more fully discussed under the genus name *Nogaus* (see p. 439). It serves here simply to emphasize the sexual differences, and to make it evident that in considering their ecology as well as their morphology most if not all of the statements must be understood as confined to a single sex. The first step in degeneration, as already noted under the Caliginæ, was the mechanical hindrance afforded by the egg strings, and the strong incentives for remaining on the body of the host. Of course the latter was the only one operating upon the male, and it did not exert much influence so long as the female retained the power of free swimming.

As, however, this power gradually weakened in the Caliginæ and still more in the Euryphorinæ, the incentive for the male to remain upon the host with the female became stronger.

And here in the Pandarinæ, where the female has become a fixed form and correspondingly degenerate, the incentive operates with its full power on the male, and we find him in the same condition as were the females of *Lepeophtheirus* and other Caligids, that is, capable of swimming freely but under ordinary conditions remaining upon the same fish, along with the female, during his entire life. While the male has thus resisted the degenerative influences so much longer than the female, yet when he once yields the transition is more rapid, and in the very next subfamily, the Cecropinæ (see p 465), we find the male degenerated into a fixed form exactly like that of the female.

[a] The three previous steps are: (1) The mechanical hindrance afforded by the egg strings and the lack of incentive to free swimming; (2) the loss of the lunules on the frontal plates, and the consequent restriction of the free scuttling motion; (3) the development of dorsal plates on the thorax segments, thereby diminishing the freedom of bodily movement.

LOCOMOTION.

The female has entirely lost the power of free swimming, and almost entirely that of moving about on her host. She can and does change her position, but only for the most strenuous reasons and during the earlier stages of development. Such motion is of necessity very slow, since it involves the loosening and refastening of the hold maintained by the different prehensile organs. Some of them must remain fastened all the time, and the only progress made is the distance that can be covered by the stretching of the body between the alternate fastenings. When removed from the fish and placed in an aquarium these females simply lie upon their backs, moving the swimming legs spasmodically, but producing no change of position at all. The males, on the contrary, can swim as freely as *Caligus*, and when placed in an aquarium with the latter they resemble them so closely in form and movements as to be distinguished only by careful scrutiny. Accordingly we should expect to find some of the males swimming about freely at the breeding season, like those of *Caligus*, and there are in the U. S National Museum collection several specimens so recorded.

None of either sex, so far as known, have lunules on the frontal plates, and hence they do not exhibit the scuttling movements characteristic of *Argulus* and *Caligus*. And yet they can move about easily and rapidly over the outside of the shark's body and are by no means confined to the immediate vicinity of the females. This motion is accomplished by means of the adhesion pads, maxillipeds, and swimming legs. The former hold the copepod to the skin of its host, while the latter push the body forward. Instead of a scuttling movement, therefore, each side of the body being advanced alternately, there is a forward gliding motion of the entire body, similar to that shown in swimming. All four pairs of swimming legs in these males are biramose, and the rami are wide flattened laminæ which propel the animal swiftly through the water.

There is no broad basal apron connecting the third legs across the mid line, which was characteristic of the Caliginæ, but this is largely compensated by the fact that the fourth legs are as broad and powerful as the third pair, while in the Caliginæ they were of no actual service for swimming.

PREHENSION.

The organs of prehension include adhesion pads, claws, and modified chelæ. The adhesion pads are common to all the genera and to both sexes; they arise as accessory organs in connection with the various appendages, and are usually of different shapes in the different genera and even in the different species, thereby affording good

supplementary means of differentiation. In the genus *Pandarus*, which may be taken as the type of the subfamily, there are four pairs of these pads (fig. 2).

The first pair are connected with the bases of the first antennæ, are elliptical or oval in outline, and stand close to the lateral margins of the carapace, sometimes even projecting beyond the margin. The second pair are connected similarly with the bases of the second antennæ, are usually circular or oval in outline, and stand inside of and posterior to the first pair. The long diameters of both pairs are parallel with the body axis, as a rule. The third pair are connected with the bases of the second maxillipeds, are sometimes circular and sometimes elliptical in outline, and stand on either side of and close to the mid line about in the center of the ventral surface of the carapace. The fourth pair arise as prominences on the bases of the first pair of dorsal plates in the female, or the lateral processes of the first free segment in the male. The exterior margin of each of these plates reaches forward under the carapace to a point opposite the bases of the first legs, and here at its antero-lateral corner the pad is developed. These pads are elongate-elliptical in outline, their long diameters parallel with or slightly inclined to the body axis. There are also in some genera pads on the basal joints of the swimming legs; these are usually elliptical, with their long diameters at right angles to the body axis (fig. 3).

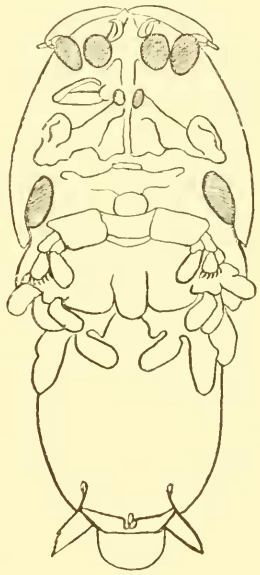

FIG. 2. VENTRAL SURFACE OF FEMALE PANDARUS SINUATUS, SHOWING ADHESION PADS.

The first two pairs of pads are the most important, and the necks or stems by which they are united to the ventral surface of the carapace are so arranged that the pads can be lowered and pressed against the skin of the host's body. The adhesive surface of the pad is formed of a thick cushion of skin whose outer layer is raised into ridges similar to those in the epidermis on the palms of our hands. These ridges are usually transverse, but are sometimes arranged concentrically, as on the tips of our fingers. They seem to serve the same purpose on these pads that they do on our hands—the development of friction and the prevention of slipping.

The claws or chelæ are found on the tips of the second maxillipeds, which are the chief organs of prehension. In the males of all the genera and in the females of some of them the second maxillipeds end in curved claws similar to those found in the Caliginæ and Euryphorinæ.

But in the females of *Pandarus, Nessipus,* and allied genera the claw disappears in the fully developed adult and in its place appears a pair of knob-like protuberances, armed with minute papillæ or scales which operate like a chela and obtain a hold by pinching a fold of skin between their inner surfaces.

Sometimes the males are also found with knobs instead of claws; the two occurring interchangeably, even in the same species.

Either of them give the copepod a firm grasp upon its host and, assisted by the adhesion pads, fasten it securely in place.

Indeed, it has been the author's experience that living specimens have to be removed with great care in order to avoid breaking their prehensile appendages. On the other hand, Hesse speaks of them in the quotation just given as "insecurely fastened to a skin which is tough and leathery." And he then adds: "They are not slow, when taken from the water, to detach themselves and fall to the ground or the bottom of the boat."

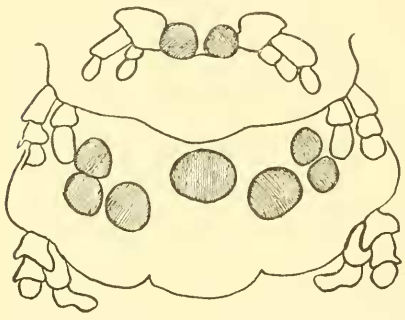

FIG. 3.—VENTRAL SURFACE OF FIRST THREE PAIRS OF SWIMMING LEGS OF ECHTHROGALEUS DENTICULATUS, SHOWING ACCESSORY ADHESION PADS.

In the experience of the present author no Pandarid has ever voluntarily detached itself; some have fallen or been rubbed off their host, but only when dead. Many scores of times, after pulling the pound-net at the U. S. Bureau of Fisheries or the Marine Biological Laboratory at Woods Hole, Massachusetts, the sharks obtained, which varied from two or three to twenty-five or more in number, have been thrown on the bottom of the boat and towed from 1 to 3 miles behind a small steamer before being examined. But on reaching the wharf the Pandarid parasites were found still clinging to them, and after careful trial it was decided that so far as sharks are concerned, the chief thing to be gained by going out to the net and removing the parasites on the spot was the chance of keeping them alive a little longer. And here again the experience of the author is different from that of Hesse, who says: "I have been able occasionally to secure them alive, but have not been able to keep them in that condition for any length of time. In this they are very different from *Caligus* and *Trebius,* and even from *Cecrops* and *Læmargus,* which I have kept alive for some time."

If he is speaking of the females this is partially true, and yet the author has repeatedly kept Pandarid females alive for several days.

But the males are always as hardy as any of the genera he mentions, and usually when placed with *Caligus* or *Lepeophtheirus* they outlive the latter.

Hesse's mistakes have probably originated from another fact which has an important bearing on the length of life in these parasites. In the Caliginæ the arched carapace acts as a large sucking disk, its margin being pressed close to the surface, made continuous posteriorly by the broad lamina connecting the third legs, and the contact sealed with water and slime.

The space beneath the carapace is filled with water, and this is often retained for a long time after the surface of the fish has become dried. Living and active specimens have often been obtained from fish whose outer surface and fins had been dried for two or three hours. On the inside of the operculum and in the gill cavity they sometimes remain alive out of water for twenty-four hours after the death of the fish.

In the Pandarinæ the carapace is not thus arched and there is nothing to continue its margin posteriorly; consequently it does not retain the water, but the latter escapes as soon as the skin of the fish dries, just as it does from beneath the cover glass on a microscope slide. As soon as the fish dries, therefore, all the Pandarids on its outer surface also quickly die, and they do then drop off, or can be brushed off very easily. For the same reason, while the sharks are being brought ashore these parasites usually become exhausted for want of moisture. And although they may still be alive when removed from the fish they do not live very long afterwards. But given a fair chance, the females are as long lived as any of the fixed parasites, while the males who do retain moisture under their carapaces in the same manner as *Caligus* and *Trebius* are fully as long lived as the latter.

This subfamily of Pandarinæ are thus clearly differentiated from the Caliginæ, Trebinæ, and Euryphorinæ on the one side and from the Cecropinæ on the other by many distinct peculiarities of morphology and habits. The most striking differences are to be found perhaps in the males, although the other sex is by no means deficient in them.

In the Caliginæ we find the sexes similar, the male usually smaller, but sometimes larger than the female. The young females, and even the adults when without egg-strings, are as active as the males, and both sexes have retained fully their power of locomotion in spite of their parasitic habits. This equality of the sexes is partially explained by the fact that neither of them carry any dorsal plates on the thorax or genital segment. The family includes one genus, *Echetus*, in which the adult female has become fixed in position, but this is due to the burying of the head and thorax in the flesh of the host.

The mouth-tube is short and broad, with a bluntly rounded tip.

First maxillæ are present in the form of short claws near the margin of the carapace; the second maxillæ are in the form of simple, slender, and acuminate spines; the furca is biramose; the first and fourth legs are uniramose, while the rami of the second and third pairs have peculiar patterns of the joints, easily recognized after a little experience.

In the Euryphorinæ the sexes are also similar, the male always smaller, more slender, and more active than the adult female. The young females, however, are still as active as the males, since they are unhindered by either egg strings or dorsal thorax plates. The presence of the latter in the adults helps to render them sluggish, and yet there is no genus which actually becomes fixed like *Echetus* among the Caliginæ.

For the other characters, the mouth tube is like that of the Caliginæ, but there are no first maxillæ nor any furca. The second maxillæ show a transition from simple pointed spines in *Caligeria*, through a blunted biramose shape in *Gloiopotes*, into a flattened lamina in *Alebion*. All the legs are usually biramose, the pattern of the rami of the second and third pairs similar to that in the Caliginæ.

In the Pandarinæ, on the contrary, the sexes are very dissimilar; the females, even when young, carry so many dorsal plates on the thorax and genital segment as to render them practically helpless. They can swim but little and quickly become stationary upon their host. But the males retain the powers of locomotion and can swim or scuttle about over their host's body with as much freedom as those of either of the preceding subfamilies. They have no trace of dorsal plates, either on the thorax or genital segment; the sex differences in this subfamily, therefore, are the greatest anywhere shown in the Caligidæ. The mouth tube is long and pointed, and the mouth parts are transformed into blade-like, smooth laminæ, without spines or setæ, or they remain rudimentary. The swimming legs are also characterized by the equality of the rami on the first pair and by a general tendency toward degeneration in the females. This usually affects only the last pair (*Dinematura* females), or the last two pairs (*Pandarus* females), but sometimes affects them all (*Demoleus* females). But whether degenerate or not their pattern is always totally different from that in the two preceding subfamilies.

Finally in the Cecropinæ we find the sexes again similar, but this time they both carry dorsal plates on the thorax and genital segments which effectually prevent free swimming. And both sexes become permanently fixed as soon as they have found lodgment on their host's body. The mouth tube is not as long as in the Pandarinæ, but is fully as pointed, while the maxillæ remain laminate and are much larger proportionally than in any preceding sub-

family. There is a tendency to degeneration in the swimming legs similar to that shown in the Pandarinæ, but while it was there confined to the female sex only it here extends to both sexes, and may even include both the third and fourth pairs of legs in the male (*Orthagoriscicola* males).

ONTOGENY.

The life histories in this subfamily are almost the same as in the Caliginæ and Euryphorinæ. The differentiation between the two must be sought chiefly in the habits and sexual characters, as already stated. The number and size of the eggs and the changes during their development are similar to those given in the preceding subfamilies. From eight to ten weeks are required for development, and

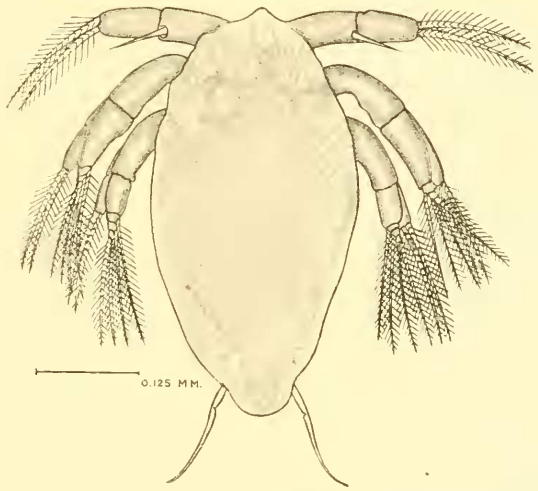

FIG. 4. A NEWLY HATCHED NAUPLIUS OF PANDARUS SINUATUS.

all the eggs in the strings of any given female hatch at practically the same time. The issuing nauplius is almost an exact counterpart of that seen in the Euryphorinæ; its body has the outline of an elongated ellipse, is well rounded anteriorly, but is somewhat contracted posteriorly through the bases of the balancers (fig. 4). The eye spot is far forward and not prominent. The three pairs of appendages are of the usual pattern and arrangement. The anterior part of the body is transparent, and inside of it can be plainly seen the muscles which move the appendages. The balancers are very long, cylindrical, and narrow acuminate; they stand out nearly at right angles to the body axis and are curved slightly forward. The central portion of the posterior half of the body is filled with opaque yolk granules, leaving a narrow transparent margin around the edge. These granules are colored a uniform and very pale brownish-yellow, and there are no

pigment spots nor any color patterns in the nauplii thus far observed, a condition very different from that found in the nauplii of the Caliginæ and Euryphorinæ.

The difficulty of hatching these nauplii and rearing them through successive molts is fully as great as in the case of the Euryphorinæ, but for a very different reason. In the Euryphorinæ the unripe female moved restlessly about the aquarium all the time, and finally crawled up out of the water and remained there until dead and dried; consequently the eggs were dried and killed before they had time to hatch. Here in the Pandarinæ, on the other hand, the female is incapable of motion, and when placed in an aquarium simply falls to the bottom and lies there inert, usually upon her back. In this way the eggs fail of proper aeration and die almost as surely as when taken out of the water and dried. Fortunately here also, as in the Euryphorinæ, the hosts are common species of sharks, and a careful examination of the gills and body of these sharks during the parasites' breeding season is practically sure to yield development stages. The eggs for most of the genera hatch about the first of July, so that the best time to look for development stages is during the middle and latter part of the month.

Those of *Perissopus* and *Pandarus* are found upon the external surface, the former on the head and especially around the mouth, the latter in the vicinity of the fins. Those of *Nesippus* are found attached to the gills, usually near the ends of the gill arches. When the nauplius molts into a metanauplius the second pair of antennæ are turned forward side by side, enlarged, and developed into long prehensile hooks, whereby the larva fastens itself to its host. At the same time the second maxillipeds become organs of attachment and materially assist the second antennæ. Both organs retain their function throughout life, the second maxillipeds usually increasing in size and efficiency until they become the chief organs of prehension in the mature adult, while the second antennæ diminish somewhat, but never lose their function entirely.

The development, therefore, is very similar to, and in fact almost identical with, that of the Caliginæ. And when the metanauplius molts into a chalimus the similarity is further increased by the fact that a frontal filament is formed, very different in length and structure from that found in the Caliginæ, but entirely similar in function.

Hesse claims (1883, p. 4) to have found a larva belonging to the "Pandaridæ," which he calls "*Nogagus spinacii-achantias*" and which he says was attached by a long and slender frontal filament to its "mother's" carapace. But when his account is examined it is found that very little can be accepted as authentic until further evidence is given.

In the first place the only reason which he can give for regarding the adult as the mother and the larva as her offspring is the fact that the latter was attached to the carapace of the former. The absurdity of drawing such a conclusion from this single premise has been already shown[a] and may be briefly restated as follows: When first hatched the nauplii swim freely at the surface; after two or three molts they seek out a suitable host and attach themselves to it. There is not one chance in a million that they will find the same host again, to which their mother is attached, and still less chance of finding the mother herself among other parasites of the same and different kinds. In fact, to find the mother at all necessitates the assumption of the ability on the part of the larva or the mother, or both, to recognize the other, which one hardly cares to concede.

Again, the individual to which this larva was attached, and which Hesse calls the "mother," is unfortunately of the male sex, as is clearly shown by his figures and description. It has the typical *Nogaus* form; there are no signs of dorsal plates on thorax or genital segment, and none of the swimming legs show any signs of degeneration. This fact renders any close relationship between the two practically impossible.

Finally, Hesse writes that this larva was 3 millimeters long and 1 millimeter wide, with a fully developed frontal filament. But he describes and figures only a single pair of swimming legs, and they are on the second thorax segment. Every metanauplius which has thus far been observed possesses at least two pairs of these swimming legs, and a chalimus 3 millimeters in length belonging to any of the subfamilies of the Caligidæ must possess at least three pairs, and ought to possess four pairs, of such legs, the first of which would be attached to the ventral surface of the carapace and not to the second thorax segment. Again, the first antennæ are represented as attached to either side of the "umbilical button" at the base of the frontal filament. They are half the length of the carapace, two-jointed, and free to their very base: in other words, the chalimus has no frontal plates. The posterior half of the body is cylindrical and five-jointed, the joints diminishing in size backward. The first of these joints carries the single pair of legs and, in addition, on its ventral surface:

> On remarque, à l'extrémité d'un article fémoral, assez long, des lames plates, denticulées sur les bords et garnies de soies, qui sont destinées à favoriser les mouvements de propulsion et de natation, et, de chaque côté de l'anneau suivant, deux lames plates, denticulées, qui sont consacrées aux mêmes fonctions (p. 6).

[a] Proc. U. S. Nat. Mus., XXVIII, p. 548.

What these "lames plates" could be would furnish something of a puzzle to the comparative anatomist.

Hesse then adds, under what he is pleased to call "Physiologie":

J'ai d'abord exprimé l'opinion que cet embryon pourrait bien être un mâle qui, joint à une femelle *adulte*, douée conséquemment de moyens de locomotion plus puissants que les siens, pouvait l'entraîner sur un autre poisson et aller ainsi, avec lui, fonder une autre colonie et contribuer par là à favoriser la reproduction et la dissémination de l'espèce (p. 31).

That is to say, a male, which is free swimming in all the *Nogaus* species, attaches itself to a female, which in every species of the Pandarinæ is fixed and helpless, in order to facilitate its locomotion from one fish to another.

Since in a description of this sort there is no hint of the family, to say nothing of the generic position of the larva, we are compelled to set it aside entirely and to get our knowledge of the development of the Pandarinæ from original sources.

THE NAUPLIUS as seen in the genera Nesippus and Pandarus.

Body an elongate ellipsoid, evenly rounded in front, but somewhat contracted posteriorly through the bases of the balancers.

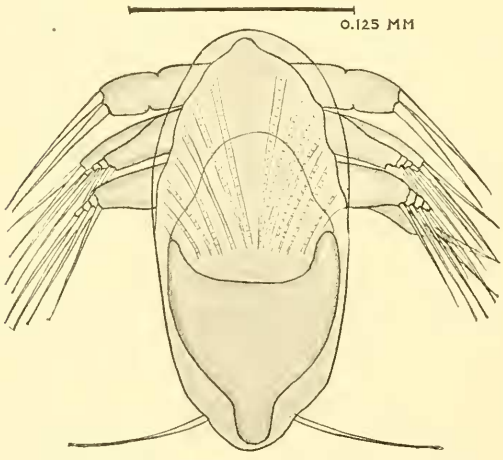

FIG. 5.—A NEWLY HATCHED NAUPLIUS OF NESIPPUS ALATUS.

The three pairs of appendages are bunched rather closely at the anterior end and are of the usual pattern. The balancers are fully one-third the entire length of the body, differing markedly in this respect from those found in the preceding subfamilies. In the *Nesippus* nauplius they take the form of simple, slightly curved, and acuminate spines; in the *Pandarus* nauplius they are slightly S-shaped, with a double curve and contracted at a point one-fourth of their length from the base, as though jointed. In *Nesippus* the color is a uniform grayish brown, with a broad, transparent, and colorless margin, and without pigment spots or other markings. (See fig. 5.) In *Pandarus* the center of the body is olive green by transmitted light, appearing cinnamon-brown by reflected light in the egg strings, or even almost black.

The transparent margin is also very irregular in pattern and width, especially opposite the bases of the locomotor appendages.

The central mass of pigment reaches forward anteriorly in a long median, two-pronged projection and sends out branches also on either side opposite the second pair of appendages and the balancers. The anterior half of the body is more or less transparent and shows the muscles plainly, while the posterior part is opaque from the presence of yolk granules (see fig. 4).

Length, 0.25 mm.; width, 0.12 mm.

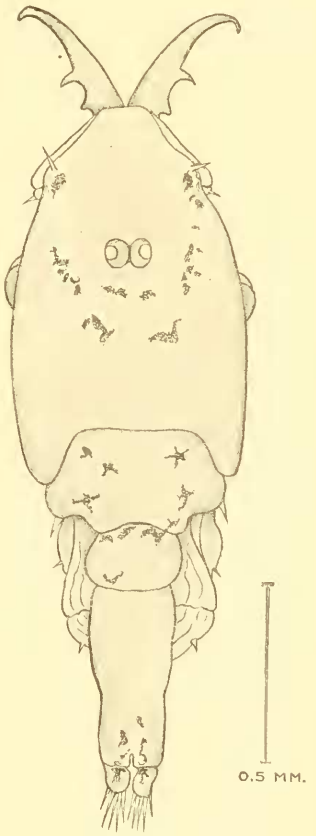

FIG. 6.—THE METANAUPLIUS OF NESIPPUS ALATUS.

THE METANAUPLIUS as seen in the genus Nesippus.

On molting from the nauplius into the metanauplius the body becomes divided into regions consisting of a carapace, two free thorax segments, and a fusion of the genital segment and the abdomen (fig. 6). The carapace has an elongated acorn shape, the length twice the width, and squarely truncated posteriorly, with the corners produced into narrow lobes reaching to the center of the first free segment. The frontal plates are large and prominent, but folded under the anterior margin, so that very little of them can be seen in dorsal view. They are folded more evenly than in the *Alebion* larva and do not leave conical projections at the anterior corners. The eyes are situated even farther back than in *Alebion*, nearly half the distance from the anterior margin. They are quite large and not fused, although in contact on the mid-line.

The first free segment is evidently a fusion of the second and third thorax segments, as is indicated by the attachment of the legs. As these two segments are more or less fused in all the adults belonging to this subfamily, their fusion here in the matanauplius is what would naturally be expected.

The fused segment is nearly as wide as the carapace, and is furnished with broad lateral lobes at the sides over the bases of the legs. Such lateral lobes or plates are also characteristic of all the adults of both sexes, but in later development they become longer and nar-

rower. The second free, which is really the fourth thoracic, segment is just half as wide as the first, with strongly convex sides.

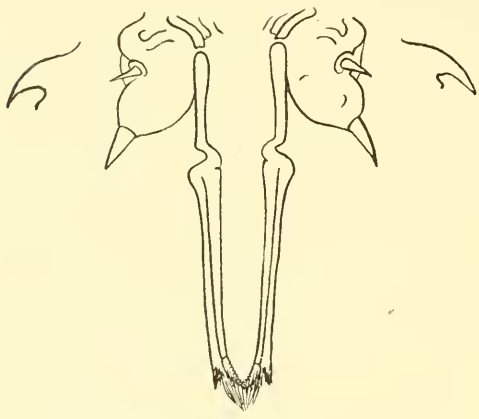

FIG. 7.—THE MOUTH TUBE, MAXILLÆ, AND MANDIBLES OF THE METANAUPLIUS OF NESIPPUS ALATUS.

The last segment, which is a fusion of the genital segment and abdomen, has the same width as the fourth thorax segment, but is three times as long and somewhat narrowed posteriorly.

The anal laminæ are relatively larger than in *Alebion*, but are tipped with much shorter setæ, five on each lamina.

The first antennæ are two-jointed, the terminal joint short and armed with small spines only, without the plumose setæ found in both the Caliginæ and the Euryphorinæ. The second antennæ are similar to those of *Alebion*, but with two stout accessory spines on the inner margin near the base.

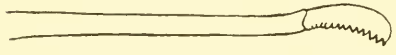

FIG. 8.—A MANDIBLE OF THE METANAUPLIUS OF NESIPPUS ALATUS.

The proboscis is also similar to that of *Alebion*, but is longer and of a more uniform width throughout (fig. 7). At its tip can be seen the mandibles, which are slender, somewhat enlarged, curved toward the free ends, and coarsely toothed along the inner concave margins. At this stage only the tips of the mandibles touch each other. Later, when the end of the mouth tube is compressed laterally, the entire toothed portion is interlocked (fig. 8).

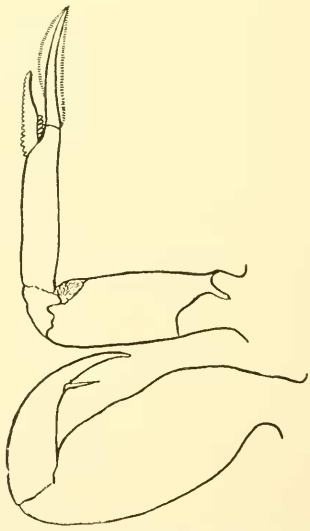

FIG. 9.—THE FIRST AND SECOND MAXILLIPEDS OF THE METANAUPLIUS OF NESIPPUS ALATUS.

The second maxillæ are close to the base of the mouth tube on either side, are simple, and consist of a stout conical base tipped with a short and stragiht spine. On the outer side of the base is another shorter spine, representing the rudimentary exopod; this rudiment is seemingly lost in later development. The first maxillipeds are slender and two-jointed,

the terminal joint narrower and longer than the basal, and tipped with two claws, the shorter ventral one with a few coarse teeth on the inner side at the base and a narrow-toothed flange along its outer margin (fig. 9). The dorsal claw is narrower and longer and has a narrow-toothed flange along either side.

The second maxillipeds are two-jointed, as in the adult, but are slender, with the terminal claw two-thirds the length of the basal joint, strongly curved, and with a small accessory spine on the inner margin near the tip.

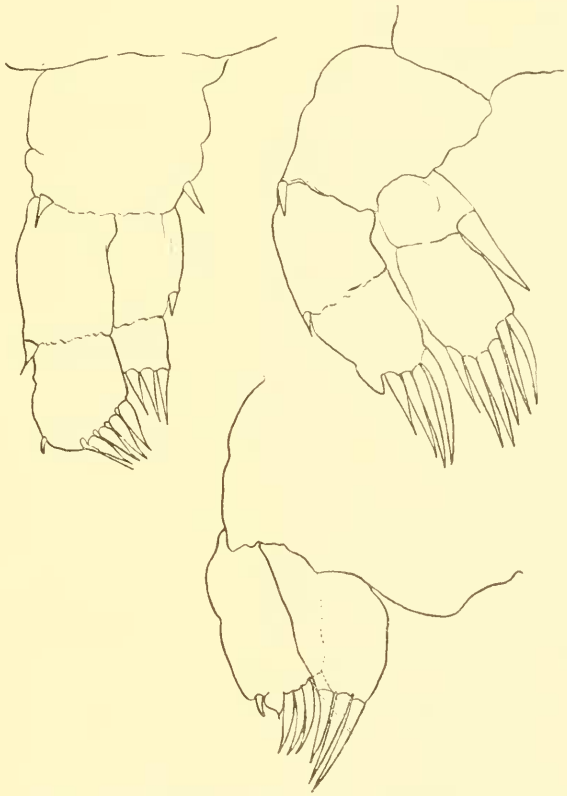

FIG. 10. THE FIRST THREE PAIRS OF SWIMMING LEGS OF THE METANAUPLIUS OF NESIPPUS ALATUS.

There are three pairs of swimming legs, all biramose; the rami of the first two pairs are indistinctly two-jointed, while those of the third pair are one-jointed (fig. 10). The basal joint of each ramus has a single spine at its distal corner, on the outside in the exopod, on the inside in the endopod, while the terminal joint is tipped with a row of large and nearly straight setæ.

This metanauplius is of a yellowish horn color, quite transparent except through the center of the body. The pigment is scattering

and consists of a V-shaped string of small spots starting at the bases of the first antennæ on either side and extending obliquely backward to meet behind the eyes.

The two free segments have a few spots irregularly arranged, and there are a few more at the posterior end of the abdomen and in the anal laminæ. These spots are all of a reddish purple color; the eyes are a deep purple with bright red lenses. Total length, including the second antennæ, 2.1 mm. Length of carapace, 1 mm. Width of same, 0.5 mm. Length of fused genital segment and abdomen, 0.51 mm.

This metanauplius stage was obtained from the gill filaments of the sharp-nosed shark, *Scoliodon terræ-novæ*, at Beaufort, North Carolina, in company with two adult females and three males of the same species. The peculiar stag-horn antennæ give these larvæ a more secure hold upon their host than in the Euryphorinæ. With such organs of prehension it would also be more difficult for the larva to loosen its hold and move about. There is thus perhaps in this larval stage an indication of the greater subsequent fixity of the adult.

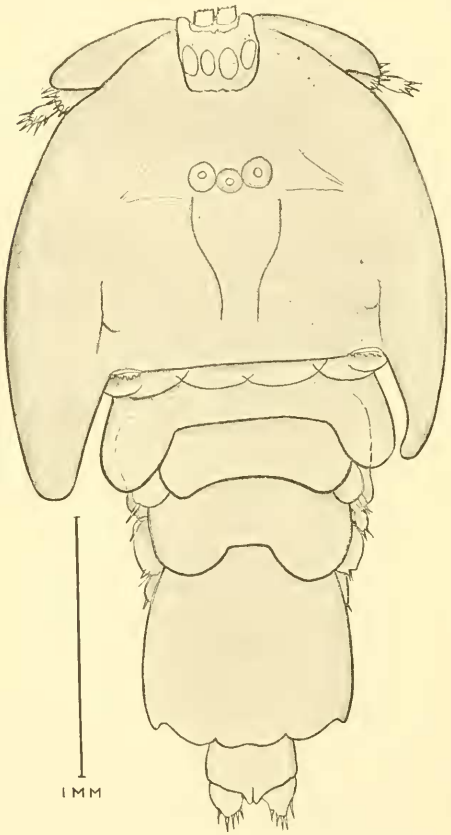

FIG. 11.—A CHALIMUS OF PERISSOPUS COMMUNIS.

THE CHALIMUS as seen in the genus Perissopus.

Only fully developed male chalimi were found, and they are described under the species *Perissopus communis* on page 357.

Single specimens of the female chalimus in three stages of development were obtained, measuring, respectively, 3, 4, and 4.5 mm. in length.

(1) In the chalimus 3 mm. long the carapace, including the posterior lobes, is semielliptical, longer than wide, and has strongly convex sides (fig. 11). The posterior lobes are long and wide, reaching back to the fourth segment, and are bluntly rounded at the tip. The frontal plates are narrow at the center and widened at the